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BINARY VARIATION IN TRADESCANTIA BRACTEATA

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Although it is peculiarly variable, *Tradescantia bracteata* is ordinarily one of the most distinctive and easily recognized of the dozen or so species which are closely related to *T. virginiana.* In addition to various minor characters, it differs from all these species by its long rhizomes which permit it to grow into large mat-like clones, even in prairie sod. Plants of this species in an experimental garden may spread to a diameter of two or three feet, while in the same period the growth of other species is to be measured by inches, if at all.

In spite of its several distinctive features, *Tradescantia bracteata* is somewhat variable in a peculiar sort of way. If one confines his study to the selections from populations which find their way into herbaria, the variation seems no more extreme or extensive than in the other widespread species of *Tradescantia.* If living populations (or mass collections) are examined, however, it will be found that they vary around two quite different centers which are illustrated in figs. 1 and 2. In the prairie populations which we have studied the bulk of the individuals are more or less similar to Type 'A'. They have unusually vigorous rhizomes and form large clones. The flowering stems are unbranched, and there are usually four long internodes above the ground level. The leaves are narrow with a peculiar yellowish cast, and the pubescence tends to be very short and scattered. The other center (Type 'B') is made

Fig. 1. Habit sketch of *Tradescantia bracteata*, type 'A.'

up of plants which tend to be characterized by broad leaves, fewer nodes to the stem, vigorous secondary branches, and a lesser capacity to spread into large clones. If collections are made only by the tens and twenties these two centers are apt

Fig. 2. Habit sketch of *Tradescantia bracteata,* type 'B.' Figs. 1 and 2 drawn to the same scale by Ruth P. Ownbey, from plants collected at Portage des Sioux, Mo.

to appear, but in every collection of 100 or more plants from the same colony they are certain to be evident.

Tradescantia bracteata is therefore unique among the American Tradescantias because it exhibits extreme *intra-regional* variation. There are other species of *Tradescantia* which show as much variation when collections are made from widely different regions within their ranges, but we have found no other species which varies in this way within single populations.

To analyze this variation, mass collections of *T. bracteata* were made at a number of points. The collection at Portage des Sioux was studied the most intensively since it was nearest the laboratory, but the general features discovered there are similar at the other points where a large population was analyzed. Extremes of the two types illustrated in figs. 1 and 2 were studied carefully, and from them an index was constructed for classifying the entire population with reference to the approach of each individual to these two types. The method was originally worked out for studying hybrid populations of *Tradescantia* (Anderson, '36) and has been found to be generally applicable to such cases. The particular characters used in this index and the values assigned to each are as follows:

Maximum width of floral leaves:

Over 19 mm.	0
Under 19 mm.	4

Sepal color:

Florid	0
Intermediate	1
Not florid	2

Stomata (under a hand lens):

More conspicuous than surrounding cells	0
Scarcely as conspicuous as surrounding cells	1
No more conspicuous than surrounding cells	2

Number of elongated internodes on the flowering stems:

2	0
3	1
4 or more	2

Branching of the flowering stem:

Unbranched	2
With sterile branches	1
Branches bearing flowers	0

This index was used in classifying four populations of *T. bracteata,* with broadly similar results in each case (fig. 3), but with significant special features. At each of these localities the species was found to be morphologically duplex. That is to say, that it fluctuated around two different centers, Type 'A' and Type 'B'. That these two types are due to inherent differences in the germplasm and not to environmental or age differences is shown by the fact that transplants have consistently maintained their original type in the experimental garden. Plants moved from various midwestern points to Boston and from the Dakotas to St. Louis have held to their original type over a period of years.

Although connected in each population by a manifold series of intermediates, the extremes when sorted out by means of the index were most surprising. Individually or as a group, the extreme plants of Type 'B' are morphologically very similar to *Tradescantia hirsutiflora* of the Gulf Coast, a species which is today completely unknown within the range of *T. bracteata.*

Tradescantia hirsutiflora (or at least one element in it) is itself so similar to *T. virginiana* that it might almost be considered a geographically localized variety of that species. While the ranges of *T. virginiana* and *T. bracteata* overlap slightly, extreme plants of Type 'B' resemble *T. hirsutiflora* more closely than they do *T. virginiana.*

In any explanation of the binary variation of *T. bracteata,* there are several critical pieces of evidence.

1. While the differences between the two types are manifold, there is enough relationship physiologically between them to suggest that there might be basically a single difference in rhizome vigor, to which all the other differences are secondary. Active rhizomes would produce large clones with many shoots, among which there would be more root competition beneath

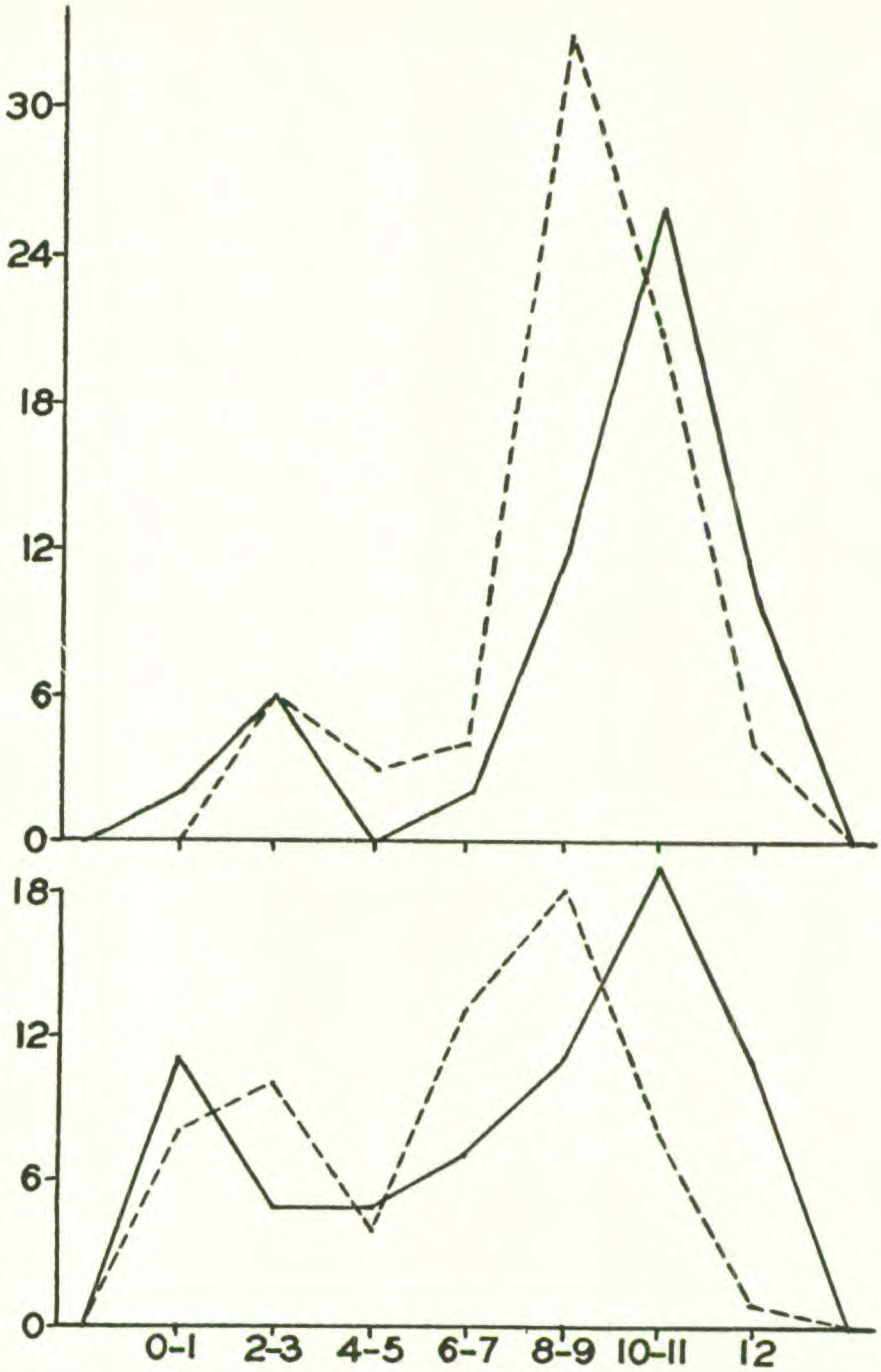

Fig. 3. Frequency diagrams for Index No. 1 of four populations of *T. bracteata*. Upper figure, from plants growing in sod: dotted line, 60 plants from unplowed swamp pastures at Portage des Sioux, Mo.; solid line, 30 plants from prairie swale at Harris's Grove, north of Grinnell, Iowa. Frequencies crudely adjusted by multiplying by 2. Lower figure, two populations from roadways: dotted line, 60 plants along roadway at edge of field, Portage des Sioux, Mo.; solid line, 60 plants from railroad right-of-way and roadway, Victor, Iowa.

the soil and more shading above the soil. It is therefore conceivable that the narrower, less-branched shoots and the narrow leaves and smaller flowers might be merely a secondary consequence of more active rhizomes.

2. Though the differences between the two types might result from a single physiological difference, there is little in the variation to suggest that it is the work of a few genes. The differences are too manifold and the variation of the intermediates resembles the varied recombinations of second-generation species crosses rather than simple Mendelian segregation.

3. The differences are apparently not due to age, since transplants of both types have maintained their original character when brought into experimental gardens. One of the clones which was originally selected because of its remarkable capacity to spread repeated this behavior when transplanted from Iowa to Massachusetts.

4. The peculiar characteristics of Type 'A' are unique in this group of species.

From this evidence we conclude that Type 'A' and Type 'B' owe their differences to segregating elements within the germplasm, to differences of the order of whole chromosomes or of chromosome arms. As to how this variation was introduced into the species we have no evidence. There are at least two very different ways in which it might have occurred. On one view, *Tradescantia bracteata* would originally have been only of Type 'B'; on the other hypothesis, the original element in the species would have been Type 'A'. It may be that the binary condition is as old as the species. On that view, the peculiarities of Type 'A' appeared within the original primitive stock of Type 'B' (by whatever process or group of processes specific differences are achieved in this genus) with the added peculiarity that the original stock tended to be carried along in the population. Quite another hypothesis is suggested by the resemblance of the variation of *T. bracteata* to that which we have studied in species hybrids of *Tradescantia*. On this view, Type 'A' was originally differentiated as a unique species and Type 'B' then originated by hybridization between Type 'A' and *T. hirsutiflora* at a time when the ranges of one or both of these species were different enough from their present distributions to bring them into contact. If this happened comparatively recently we might expect to find Type 'B' limited to the southern or southeastern extremity of the range of

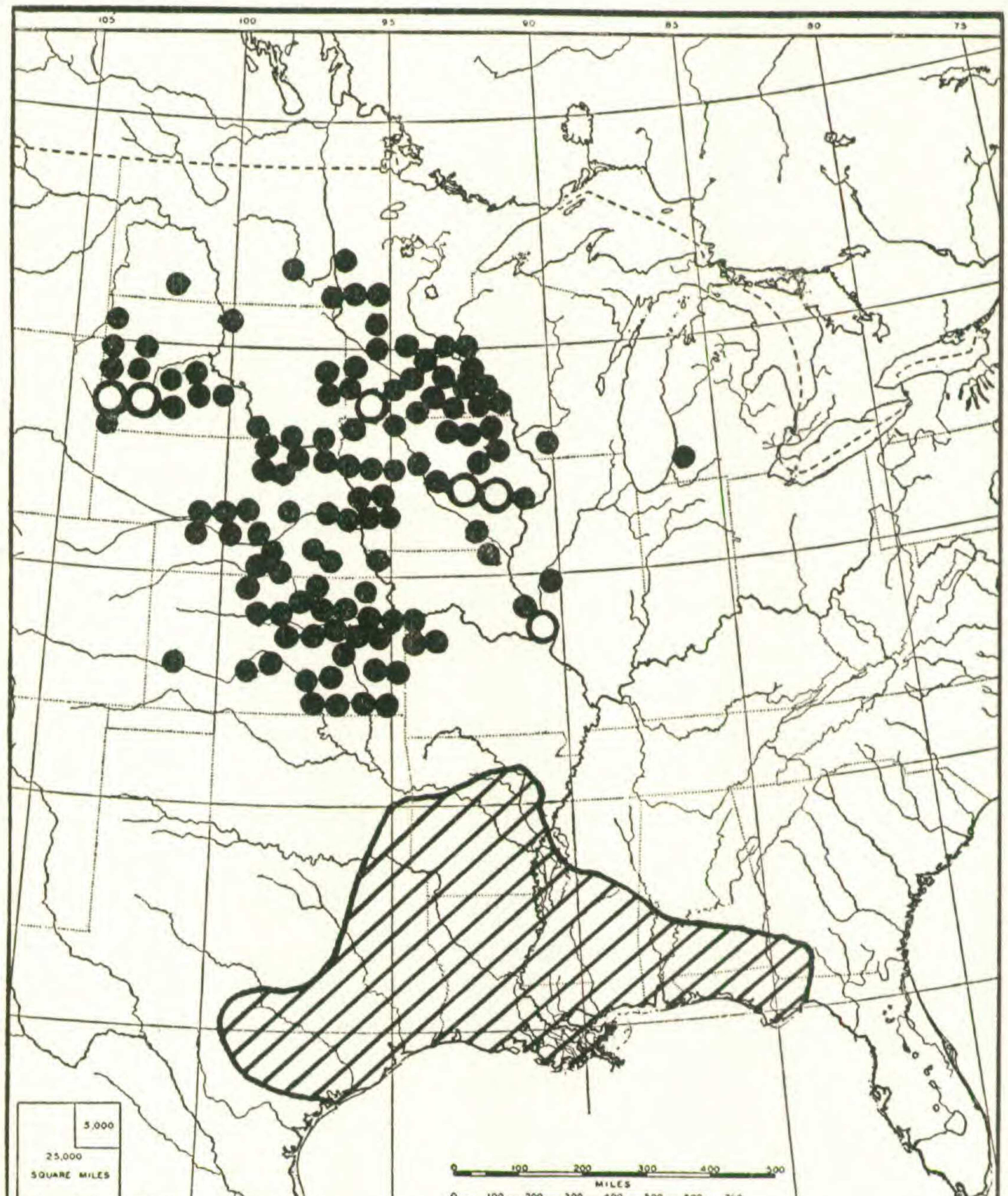

Fig. 4. Map of middle-western United States showing the known distribution of *T. bracteata* (black dots) in relation to that of *T. hirsutiflora* (diagonal lines). Each dot represents an herbarium specimen; open circles, points at which mass collections were made.

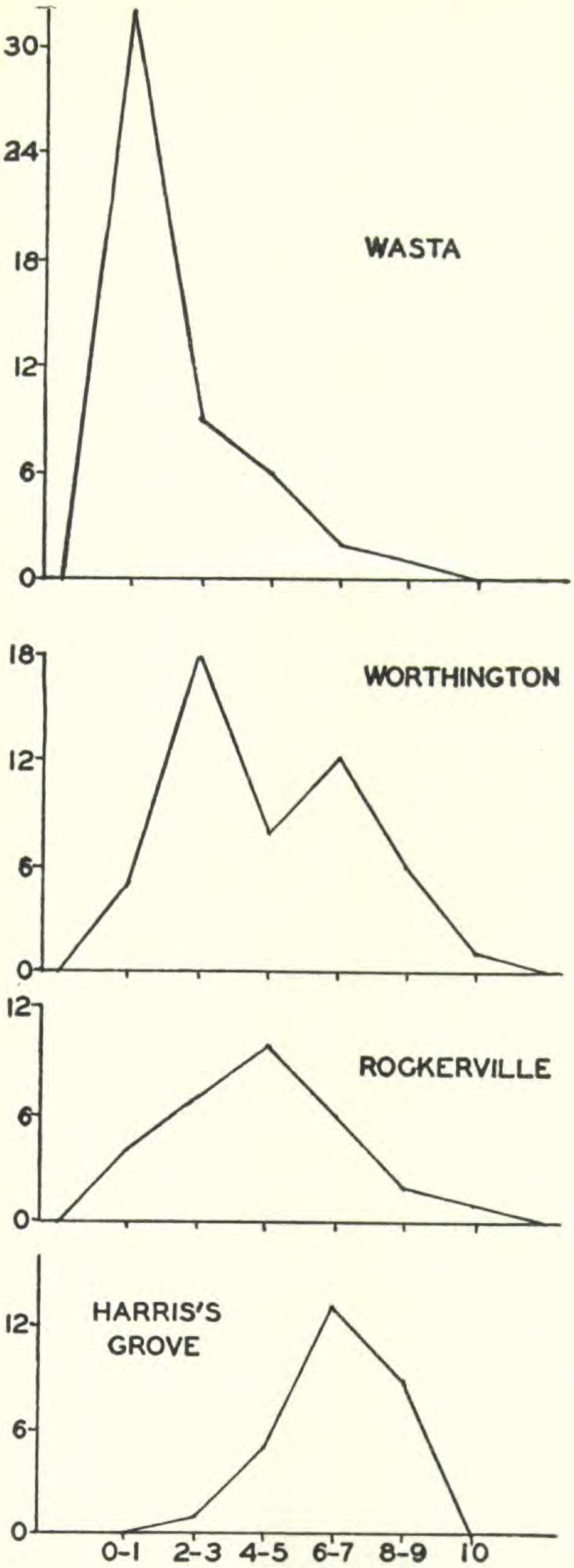

Fig. 5. Frequency diagrams for Index No. 2 of four populations of *T. bracteata.* Populations arranged according to the percentage of open soil in the habitat.

T. bracteata. If, however, the hybridization is a matter of very long standing, then Type 'B' might be expected to occur throughout the range of *T. bracteata.* For determining this point collections from the Black Hills would be particularly significant since they are at the opposite end of the range of *T. bracteata.* Mass collections were accordingly made at the points shown in fig. 4. Frequency distributions for these collections are shown in fig. 5. The index used in deriving the frequencies for fig. 3 could not be used since it was based in part on characters which can be scored only in living material. The following index was therefore constructed for dealing with the pressed material:

Maximum width of floral leaves:

From mid-vein to margin, over 8 mm.	0
From mid-vein to margin, 6–7 mm.	1
From mid-vein to margin, 5 mm. or less	2

Length of hairs on pedicel:

Over 0.8 mm.	0
0.5 to 0.7 mm.	1
Less than 0.5 mm.	2

Number of elongated internodes on flowering stems:

2	0
3	1
4 or more	2

Branching of the flowering stem:

Unbranched	2
With sterile branches	1
Branches bearing flowers	0

It will be seen that this index differs from that previously used in the following ways: (1) In measuring the maximum width of the floral leaves (bracts) one-half the width rather than the whole width had to be used because the specimens were pressed. This, as well as the changes in drying, increases the percentage of error. (2) The color of the sepals and the character of the stomata could not be ascertained in pressed material. In their place the length of the pubescence of the pedicel was substituted, since it is prevailingly thick and long in Type 'B' and short and scattered in Type 'A.' It was measured to a tenth of a millimeter, using a camera lucida. The measurement was accurate, but a study of plants in the experimental garden has shown that this character is affected by temperature and humidity. Index No. 2 therefore, while it is more or less similar to Index No. 1, is not as accurate, and since it is based on fewer characters does not separate the two centers as well in the frequency distributions. However, it gives a roughly similar result as will be seen from fig. 6, which shows

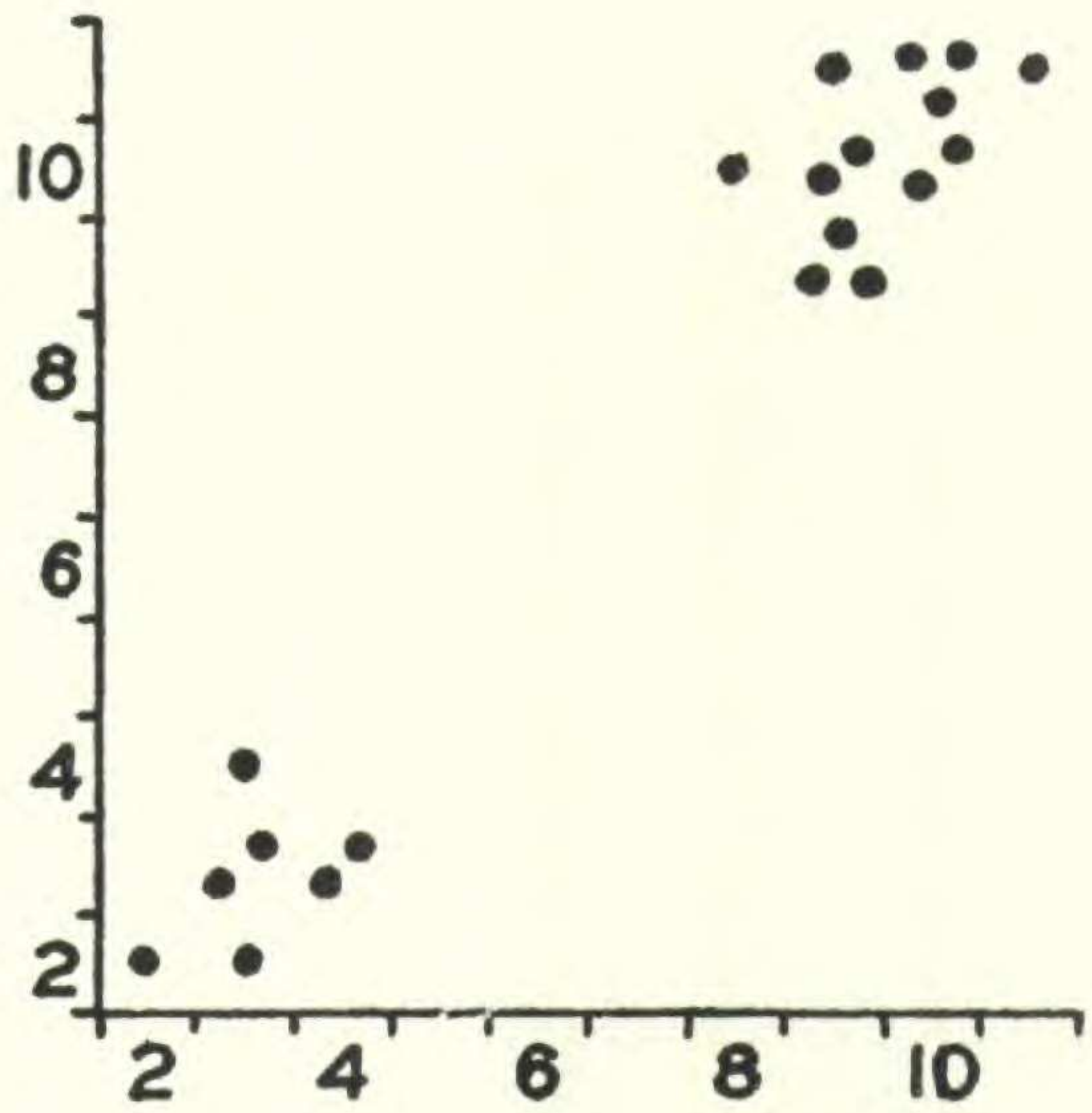

Fig. 6. Correlation between index values of 20 plants from Portage des Sioux as measured by Index No. 1, vertical scale, and Index No. 2, horizontal scale.

the correlation between the two indices for 20 plants which were measured by each index.

Population frequencies for Index No. 2 are graphed in fig. 5. It will be seen that Type 'B' not only occurs in the opposite corner of the range of *T. bracteata* from that which comes closest to the territory of *T. hirsutiflora* but that it even makes up a higher percentage of the population than it does in the south. This is perhaps correlated with open-soil habitats and is discussed below on page 159. The curves are also less bimodal than in the Missouri and Iowa populations. This is in part due to the inferiority of the index but probably also reflects a real difference in the northwestern populations. However, although plants of Type 'A' were not present in large enough numbers to produce a bimodal curve, at least a few were encountered at every locality as well as various intermediates. Type 'B' therefore most probably originated before *T. bracteata* moved into the territory it now occupies. The entire group of species to which it belongs is centered upon the Edwards Plateau in east-central Texas. It is quite possible that at one time *Tradescantia bracteata* grew within this same general area and could then have differentiated from, or hybridized with, *T. hirsutiflora.* This latter species still occurs there and is the most aggressive species in that area and the one most apt to hybridize with other species.

To summarize: Associated with typical *Tradescantia bracteata* throughout its range and connected with it by a manifold series of intermediates is a *Tradescantia* morphologically very similar to *T. hirsutiflora,* a species of the Gulf Coastal Plain. It is suggested that this variant originated by partial differentiation from, or hybridization with, *T. hirsutiflora* at a time when the two species were in closer contact than now, and presumably before *T. bracteata* moved into the territory it now occupies. Since the chief effect of the phenomenon is to produce a species which fluctuates around two centers, instead of one, we are calling it *binary variation.*

There now remains to discuss:

(1) Its selective advantages.

(2) The cytology of *T. bracteata.*

(3) Its probable occurrence in other groups of organisms.

(1) *The selective advantages of binary variation.*—As will be seen from the map in fig. 4, *Tradescantia bracteata* is a species of the prairies and northern great plains. This region is notorious for a climate which fluctuates widely from decade to decade as well as from year to year, and within that area *Tradescantia bracteata* is most commonly found in marginal habitats which are peculiarly susceptible to climatic fluctuations. In the prairie states it grows at the edges of swales or in slight depressions which are just damp enough to discourage

some of the prairie grasses. A single dry year has a marked effect upon the vegetation. In a fluctuating climate, in such a habitat, a species which varies around two centers would be at a great selective advantage, particularly if the permanence of the two-centered condition was assured by some cytogenetic mechanism. In this connection the frequency curves of fig. 3 are rather suggestive since they demonstrate that with a slight change in habitat there are changes in the proportions of Type 'B'. Two populations were studied in Missouri and two in Iowa. In each case one of the populations was from a more or less natural prairie and the other was from a man-made habitat. At Portage des Sioux, Missouri, in rich bottomland near the junction of the Mississippi and Missouri rivers, is a low grassy pasture which is apparently a remnant of one of the river-bottom savannahs once common to the region. One collection was made in the pasture and another along a cart track which ran beside it. Of the Iowa collections, one was from the edges of a grassy swale in an unplowed pasture and the other from along a railroad track adjacent to rich bottomland, all of which was under cultivation. It will be seen that the curves of the two prairie habitats are very similar, as are also those of the two trackways, but that the proportion of Type 'B' is much higher in the open-soil habitats, so much so that the make-up of the species differed much more markedly between neighboring habitats than it did between Missouri and Iowa, for the same habitat.

This impression is confirmed by the frequencies for Index No. 2, diagrammed in fig. 5, where they are arranged from above to below according to the prevalence of grass at each locality. At Wasta, North Dakota, there was practically no grass, and many of the plants of *T. bracteata* were growing in soil as open as if they had been cultivated in a garden. At Harris's Grove, the other extreme, the plants were growing in dense prairie sod and were so overtopped by the grass that they were hard to find. The frequency diagrams show that the grassier the habitat, the greater the percentage of Type 'A' and intermediates resembling it. This is not surprising since in at least two ways Type 'A' is evidently better adapted to such an environment. In the first place, its longer, more numerous internodes allow it to compete for sunlight with the grasses in situations where plants of Type 'B' would be completely submerged. In the second place, its extremely active rhizomes would allow it to compete with the notoriously vigorous rhizomes of the prairie grasses.

(2) *The cytology of T. bracteata.*—*Tradescantia bracteata* is prevailingly diploid, with 6 pairs of chromosomes. Table I lists the chromosome determinations which have been made as well as those previously listed by Anderson and Sax ('36) and summarizes the total frequencies. The species is overwhelmingly diploid, although polyploid individuals have been collected in nature at two points. It is therefore unlike all the other widespread species closely related to *T. virginiana,* since they are either known only as tetraploids or have diploid races confined to a relatively small area. There are other diploid species in this group but, without exception, they are of very limited distribution and several of them are on the verge of extinction. In our opinion diploidy has persisted in *T. bracteata* because it is actually at a selective advantage in prairie habitats by reason of its effect upon the flowering season. Like many other prairie plants, *Tradescantia bracteata* dies down rapidly after it has flowered and spends the summer in a dormant or semi-dormant condition. In an experimental garden

TABLE I

CHROMOSOME NUMBERS OF PLANTS OF *T. BRACTEATA* COLLECTED IN THE WILD

Localities	2n	3n	4n	Localities	2n	3n	4n
Houlton, Wisconsin	1			St. Louis, Missouri	1		
Preston, Minnesota	1			Huron, South Dakota	1		
Rock Co., Minnesota	1			Kennebec, S. Dak.	1		
Worthington, Minn.	1			Murdo, S. Dak.	1		
Grinnell, Iowa	3	2		Rockerville, S. Dak.	1		
Kellogg, Iowa	1			Wind Cave, S. Dak.	1		
Kendallville, Iowa	1			Wasta, S. Dak.	2		
Pierson, Iowa	1			Overton, Nebraska	1		
Tama, Iowa	3			Royal, Nebraska	1		
Victor, Iowa	1			Lawrence, Kansas			2
Portage des Sioux, Missouri	8			Manhattan, Kansas	3		

it withers so quickly that one who did not know the species would assume that the plants were badly diseased. Tetraploidy would be disadvantageous to such a species since it favors longer flowering seasons. In nature, in the experimental garden, and in the greenhouse, tetraploid Tradescantias differ from their related diploids, among other things, by the greater length of their blooming periods. Polyploid strains, such as the plants reported in Table I, would be at a selective disadvantage since they would come into flower more slowly and carry their flowering into the unfavorable drought and heat of the summer months. The two tetraploid plants reported above were discovered under precisely those circumstances. When originally collected they were the only plants still in flower at that locality, all the neighboring plants having withered and died down.

Aside from the gross information concerning chromosome number, little is known with regard to the cytology of *T. bracteata.* Sax ('37) and Darlington ('37) have reported inversions in this species, and Swanson ('40), from these facts and his own evidence, has concluded that the occurrence of inversions in *Tradescantia* is very widespread.

The fact that both Type 'A' and Type 'B' have been found in every population which has been examined leads us to suspect that the binary condition is being maintained by some fairly precise cytogenetic mechanism. Otherwise it is difficult to see how both varieties could be present in every population. There must at least be some mechanism by which plants which are phenotypically like one variety can yield offspring resembling the other when they are intercrossed. One would need to postulate no more intricate mechanism than those already demonstrated for cereal rogues or the complexes of *Oenothera.*

Although the morphological differences between the two species seem to be manifold, it is possible, as we have pointed out above, that only a small proportion of the germplasm is responsible for the change. Given the basic difference in rhizome growth, many of the other differences might automatically follow. A large matted clone with many flowering stems might be expected to have narrower leaves and less secondary branches than an isolated plant such as Type 'B,' with only a few flowering stems. If only one or two chromosome segments are responsible for the bulk of the differences between the two varieties it would be comparatively easy for the binary condition to be maintained.

(3) *Probable occurrence of binary variation in other groups of organisms.*—Binary variation, in our opinion, is probably fairly widespread in both the plant and animal kingdoms. Its frequency can scarcely be discussed until more species have been examined by populations. Up to the present not more than a handful of species has been studied in this way. Certain of the Drosophilae studied by Dobzhansky, Spencer, Patterson, and their students are perhaps to be classified in this category though data with regard to populations are still too meagre to permit a definite opinion. The relationship between the black and white races in the southeastern United States is very similar and differs only in the fact that there are numerous communities which fluctuate around only one center and that the chief isolating factor (social prejudice) has caused nearly all the intermediates to be classified as black instead of being recognized as intermediates.

Among the higher plants binary variation probably occurs fairly frequently within a part of the range of widespread species, but cases such as *T. bracteata* where a species is binary throughout its range are probably rare. In eastern North America many, if not most, of the deciduous trees which are relatively uniform in the North and East include other elements within their populations in the Ozarks and the Southwest. *Acer saccharum,* for instance, forms relatively uniform populations to the northeast, while in the Ozarks usually it includes the variety *Schneckii* and is united with it in that region by a series of intermediates.

SUMMARY

1. Associated with typical *Tradescantia bracteata* throughout its range and connected with it by a manifold series of intermediates is a *Tradescantia* morphologically similar to *T. hirsutiflora.*

2. It is suggested that this variant originated by partial differentiation from, or hybridization with, the *T. hirsutiflora-virginiana* stock at a time when the ranges of these Tradescantias were confluent.

3. The phenomenon is named "binary variation." Its selective advantages and probable occurrence in other species are discussed.

4. The cytology of *Tradescantia bracteata* is discussed. It is suggested that the exceptional maintenance of widespread diploidy in this species is due to the fact that in a prairie and great-plains environment the shorter blooming season of the diploids may be at a selective advantage.

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